BODY TEMPERATURES OF WHITE-FOOTED MICE IN RELATION TO ENVIRONMENTAL TEMPERATURE AND HEAT AND COLD STRESS ¹

JOHN A. SEALANDER, JR.

Department of Zoology, University of Arkansas, Fayetteville, Arkansas

Many mammals are completely homoiothermic only with a relatively narrow range of external temperature, particularly some of the more primitive mammals which, with respect to thermoregulatory ability, are intermediate between the true poikilotherms and the more highly evolved mammals (Britton and Atkinson, 1938; Kredl, 1928; Martin, 1930; Morrison, 1945, 1946; Sutherland, 1897; Wislocki and Enders, 1935). Body temperatures of more advanced mammals are influenced by changes in air temperature but do not undergo the wide fluctuations that are characteristic of primitive mammals (Gaalaas, 1945; Seath and Miller, 1946). Among mammals the bats seem to be distinct in that, except during periods of activity, they appear to be essentially poikilothermic (Hock, 1951; Reeder and Cowles, 1951).

As a group the rodents show varying degrees of perfection of thermoregulation. The most labile temperatures are generally found among the hibernating species, although some non-hibernators also have inconstant body temperatures (Morrison and Ryser, 1951; Wade, 1930; Wislocki, 1933). The term "heterotherm" has been applied to certain rodents and other mammals which show rather wide fluctuations in body temperatures in relation to the ambient temperature as contrasted with the more perfectly regulating homoiotherms.

Various investigators have attempted to relate body temperatures of rats and mice to air temperatures and have pointed out differences due to both air temperature and sex (Bierens de Haan, 1922; Hart, 1951a, 1951b; Herrington, 1940; Morrison and Ryser, 1951; Przibam, 1917; Summer, 1913).

Early studies on the effect of previous acclimation at high and low temperatures on the thermoregulatory ability of rodents and other mammals are few (Gelineo, 1934, 1940; Schwabe, Emery and Griffith, 1938). Only within recent years has this problem been studied intensively (Adolph, 1950, 1951; Adolph and Lawrow, 1951; Scholander *et al.*, 1950; and others). However, many of the mechanisms involved in acclimation to heat and cold still remain obscure.

METHODS AND MATERIALS

The mice used in this study were northern white-footed mice, *Peromyscus leucopus noveboracensis* (Fischer), which were trapped from wild populations in the vicinity of Champaign-Urbana, Illinois, during 1947 to 1949. All individuals were acclimated in the laboratory at temperatures from 20–24° C. for periods of 20–30 days before any body temperature measurements were made.

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The temperature chambers used in these experiments have been described in a previous paper (Sealander, 1951a).

Deep body temperatures were measured with a portable indicator potentiometer using fine copper-contantan thermocouples. The usual practice was to insert the thermocouple into the animal's esophagus, since it was presumed that possible damage to internal tissues might be less and because less difficulty was experienced in securing temperatures in this way. Thermocouples were periodically checked for accuracy against a standard thermometer.

As activity exerts an appreciable influence on body temperature (Britton and Kline, 1939; Bullough, 1949; Hart, 1951a; Kendeigh, 1945), a sufficient number of records was usually obtained to secure both maximum and minimum temperatures. A series of temperatures was taken at about one-minute intervals until no further changes in temperature could be detected for several minutes. Temperatures were recorded while the animal was held in the left hand or confined in a small cone of wire netting. The animals were handled with a glove to minimize any changes in body temperature due to radiation or conduction of heat from the handler. The mice struggled briefly when the thermocouple was inserted and then became quiet. If they continued to struggle no additional readings were taken. Body temperatures were almost invariably highest during the first minute or two of recording and then underwent only minor fluctuations during the remaining period of measurement. After the initial rise, body temperatures continued to decline gradually and usually from 8-12 minutes elapsed before they remained constant. Body temperatures of mice subjected to low temperatures were recorded within about a ten-minute period to preclude any rise in temperature from exposure to warmer room temperatures. Body temperature readings followed the same general pattern in these mice.

Automatically recorded subcutaneous temperatures of mice at different air temperatures were obtained with thermocouples inserted under the skin (Sealander, 1951b) which were connected to a strip-chart potentiometer that recorded the balance point of the circuit every three minutes.

EXPERIMENTAL RESULTS

Behavior responses. Reactions of individual white-footed mice to temperature stress were, in general, quite similar to those which have been frequently reported for laboratory rats, mice, hamsters and guinea pigs.

Initial exposures at moderately low temperatures $(-10^{\circ} \text{ to } -15^{\circ} \text{ C})$ were accompanied by periods of gnawing at the cage alternating with vigorous grooming movements. Motor activity was evidenced by frequent exploratory trips to different corners of the cage. Lowering the temperature to about -20° C. intensified these behavior responses for a short while, but gnawing and motor activity soon became infrequent although grooming movements persisted. At air temperatures between -20° and -30° C. there were only occasional outbursts of motor activity in the form of running.

Erection of the fur and reduction of the amount of exposed surface by curling into a ball became more prominent as the mice became quiet. Frequent turning movements were made, apparently in an effort to achieve a more compact body surface. At very low temperatures $(-25^{\circ} \text{ to } -35^{\circ} \text{ C}.)$ the feet, ears and tail quite often became frost-bitten due to greater exposure and contact with cold surfaces.

Polypnea and shivering were characteristic responses to cold. Their onset varied with individual mice and with the suddenness of exposure to low temperatures. Rapid breathing and shivering movements were most prominent at very low temperatures but appeared rather abruptly in mice that were suddenly placed at temperatures of about -20° C. Respiration became weak and shallow and shivering disappeared in hypothermal mice. Loss of equilibrium appeared with the approach of the lower lethal body temperature, and the lethal point was often marked by a final weak burst of activity followed by a total loss of balance and culminated in a clonic-tonic convulsion of the type described by Frings and Frings (1952).

At temperatures of 25° C. and above the mice decreased their motor activity and generally assumed sleepy, relaxed postures. When air temperature was around 35° C. the extremities became noticeably suffused with blood. At 40° C. motor activity was usually quite pronounced during the first half-hour of exposure but then ceased almost entirely. The mice salivated quite freely at this temperature and often assumed a partially erect posture with the forepaws resting upon the sides of the cage. In the neighborhood of 50° C. crawling movements were evident and the belly fur became streaked and matted with saliva as the mice crawled over the bottom of the cage.

Death occurred very rapidly in the range of temperature between 40° and 50° C. but was not accompanied by the convulsive seizures and anoxic symptoms noted at low temperatures.

Minimal recoverable body temperatures. The extremes of low temperature which many species of mammals can endure for a short period of time and still survive are often very great. For example, the laboratory rat is able to maintain a constant body temperature for several hours at -30° C. (Giaja and Gelineo, 1933). Many species of arctic mammals are notably resistant to cold as pointed out by Scholander and his associates (1950).

A number of experiments have been performed (Barbour *et al.*, 1943, 1944; Britton, 1922; Britton and Atkinson, 1938; Haterius and Maison, 1948; Luyet and Gehenio, 1940) in which mammals were subjected to very low temperatures and underwent recovery. In the majority of mammals body temperatures from about 14° to 20° C. were the lowest which could be tolerated for any length of time with complete spontaneous recovery at room temperatures, but bats and ground squirrels tolerated body temperatures from a few tenths to about two degrees below 0° C. Other mammals, such as hamsters (Adolph, 1951; Adolph and Lawrow, 1951), tolerate body temperatures as low as 4° C. for varying lengths of time.

Very few minimal recoverable body temperatures have been determined for different species of mice. Summer (1913) exposed white mice to air temperatures of -2° to 2° C. for about five hours and noted complete recovery of two mice from temperatures of 20.6° and 12.5° C. after exposure to an air temperature of 28.5° C. Kendeigh (1945) reported the recovery of a white-footed mouse, *Peromyscus maniculatus gracilis*, after its body temperature had fallen to 23.4° C. after several hours exposure in a trap.

In the present study no systematic attempt was made to determine minimal recoverable body temperatures but a few incidental observations were obtained. Two male white-footed mice exposed to air temperatures from -12° to -23° C. had body temperatures of 10° and 23° C., with exposures of 65 and 80 minutes, respectively, when removed to room temperatures of 26–27° C. Both underwent complete spontaneous recovery. Another male exposed to -20° C. for 70 minutes underwent partial recovery from a body temperature of 6° C. when removed to a room temperature of 27° C. but subsequently died. These few records indicate that this species probably falls within the general range of tolerance for non-hibernating rodents of the same general size class. There was little or no activity by the mice during the time they were exposed to the low temperature.

Lethal temperatures. Upper and lower air temperature limits between which mammals can remain completely homoiothermal over long periods of time are but incompletely known for many species. In general, these limits vary with the animal's total heat production and the degree of body insulation.

TABLE I

| Esophageal temperatures of nineteen adult Peromyscus leucopus no | veboracensis |
|--|--------------|
| at room temperatures of 25° to 28° C. | |

| | Fem | ales | | | Ma | les | | |
|----------------------|---------|----------------|------|------------|---------------------|---------|------|--|
| Number of records | Te | mperature in ° | С. | Number | Temperature in ° C. | | | |
| | Minimum | Maximum | Mean | of records | Minimum | Maximum | Mean | |
| 1 |] | 38.7 | | 10 | 35.8 | 39.2 | 37.0 | |
| 8 | 35.5 | 39.0 | 38.3 | 1 | _ | 38.2 | _ | |
| 1 | | 39.5 | | 9 | 37.0 | 40.5 | 38.2 | |
| 9 | 37.5 | 39.6 | 37.9 | 11 | 36.0 | 38.7 | 37.3 | |
| 8 | 37.3 | 39.8 | 38.5 | 9 | 35.5 | 39.3 | 37.4 | |
| 10 | 36.8 | 40.5 | 38.3 | 8 | 38.7 | 39.5 | 38.9 | |
| 10 | 37.2 | 39.7 | 38.1 | 10 | 36.0 | 39.0 | 37.5 | |
| 12 | 36.3 | 38.7 | 37.7 | 12 | 35.7 | 37.8 | 37.0 | |
| 110 | 35.7 | 40.2 | 38.2 | 12 | 36.1 | 37.6 | 37.3 | |
| | | | | 108 | 35.4 | 38.3 | 37.7 | |
| Mean | 36.6 | 39.5 | 38.1 | | 36.2 | 38.8 | 37.6 | |

Rodents are known to be much more susceptible to high temperatures than many other mammals. The usual explanation for this greater susceptibility is their lack of sweat glands, coupled with a high respiratory rate that cannot be increased greatly for cooling.

A series of esophageal temperatures taken on 15 adult *Peromyscus leucopus*, of both sexes, at the moment of death as indicated by the last convulsive respiratory movement, gives some indication of the lower lethal body temperature for this species. The mice were subjected to temperatures ranging from -12° to -35° C. while deprived of food and water. Lower lethal body temperatures ranged from 3.5° to 5.0° C. with a mean of $4.6^{\circ} \pm .5^{\circ}$ C. In general, the duration of exposure before death occurred showed a progressive increase (45 minutes to 8.5 hours) with rise in temperature. However, there was no evident correlation between the lower lethal body temperature and either air temperature or length of exposure. Inasmuch as body temperature changes rapidly after thermogenic ability is once lost it is difficult to fix an absolute lethal temperature. Heat production is probably permanently impaired in deer mice at body temperatures in the neighborhood of 10° C. as evidenced by lack of permanent recovery from temperatures in this vicinity.

A few experiments were performed in which deer mice were subjected to falling or gradually lowered air temperatures. In all cases the body temperature underwent the most rapid decline when the ambient temperature was around -12° to -15° C. All of the animals concerned in the experiments were freshly caught summer animals. Although it would appear that this is a critical zone of temperature for summer animals it seems probable that the critical zone might be lower for animals previously acclimated at low environmental temperatures.

TABLE II

| Sex | Body Temperature (° C.) | | | | | | | | |
|-----------------|--------------------------------|----------------------------------|---|----------------------------------|--|--|--|--|--|
| | Under light anaesthes | sia at point of recovery | Two hours after recovery from anaesthesia | | | | | | |
| | Mean esophageal temperature | Mean subcutaneous temperature | Mean esophageal temperature | Mean subcutaneous temperature | | | | | |
| F. | 37.1(3) | 35.9(3) | 38.4(4) | 37.2(4) | | | | | |
| Μ. | 36.7(4) | 35.5(4) | 37.5(5) | 36.0(5) | | | | | |
| F. / | 36.5(5) | 35.3(5) | 37.6(5) | 35.9(5) | | | | | |
| Μ. | 37.5(5) | 37.1(5) | 37.8(5) | 37.0(5) | | | | | |
| Μ. | 36.7(5) | 35.0(5) | 38.2(4) | 36.9(4) | | | | | |
| F. | 37.5(4) | 36.1(4) | 38.3(5) | 37.1(5) | | | | | |
| М. | 36.9(4) | 35.5(4) | 37.0(5) | 36.1(5) | | | | | |
| Mean | 37.0 | 35.8 | 37.8 | 36.6 | | | | | |
| Mean difference | 1 | .2 | 1.2 | | | | | | |

Comparison of esophageal and subcutaneous temperatures of seven adult Peromyscus leucopus noveboracensis at 25° C. when under anaesthesia* and when fully recovered**

* Sodium pentobarbital (Nembutal).

** Numbers in parentheses indicate number of records averaged. Readings taken at approximately half-minute intervals.

In experiments which involved a male and a female deer mouse, brief attention was given to the effect of high air temperatures on body temperature. These mice were exposed to air temperatures ranging from 40° to 50° C. for varying lengths of time. These experiments indicated that the upper limit of body temperature which could be tolerated for any length of time by *Peromyscus leucopus* was somewhere between 42° and 43° C. Apparently such high body temperatures can be tolerated for only brief periods without permanent impairment of temperature regulation. Exposure to temperatures of 45° and above resulted rather rapidly, usually in the space of about one-half hour, in impairment of thermoregulation. No return to normal body temperatures took place after exposure to air temperatures of 45° to 50° C. Non-reversible upper lethal temperatures between 43° and 44° were obtained for both of the experimental animals. These results are in general accord with those for the rat (Adolph and Lawrow, 1951) and for similar sized mice (Bodenheimer, 1949; Fuller and Hiestand, 1947).

Normal body temperatures. A series of esophageal temperatures was taken on several individual mice at non-stimulating air temperatures (Table I). The minimum or lowest reading obtained for each individual is considered to represent resting conditions, while the mean possibly indicates body temperatures of mice when in an active state and performing various routine activities in their natural environ-

| Т. | AB | LE | 11 | 1 |
|----|----|----|----|---|
| | | | | |
| | | | | |

Esophageal temperatures of Peromyscus leucopus noveboracensis in relation to air temperature with and without food and water

| | | | Hour of Exposure | | | | | | | | | | |
|--|-------------------|--|--|------|--------------|--------------|--------------|------|------|--------------|--------------|--------------|------|
| Mean air temper- ature (° C.) | Sex and number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| (0.) | | Mean esophageal temperature with food and water provided | | | | | | | | | | | |
| - 30 | M 10b | 30.5 | 20.1 | 10.2 | | | | | | | | | |
| - 30 | F 7c | 32.7 | 23.4 | 9.9 | | | | | | | | | |
| -20 | F 8c | 38.7 | 38.3 | 38.4 | 38.2 | 38.1 | 38.0 | 37.9 | 38.0 | 38.2 | 38.1 | 38.0 | 38.1 |
| -20 | F 9c | 38.0 | 38.1 | 38.2 | 38.4 | 38.5 | 38.2 | 38.0 | 38.1 | 37.9 | 37.7 | 37.8 | 37.9 |
| -14 | M 11b | 37.6 | 37.6 | 37.8 | 37.4 | 37.8 | 37.9 | 38.0 | 38.1 | 38.1 | 38.0 | 37.9 | 37.9 |
| -14 | F 10c M 12b | 38.0 | 38.1 | 37.9 | 38.2 | 37.9 | 37.7 | 37.8 | 37.9 | 37.8 | 37.7 | 37.9 | 37.9 |
| -1 -1 | M 120 M 13b | 38.1 | 38.2 | 38.0 | 38.4 | 38.3 | 38.5 | 38.2 | 38.1 | 38.0 | 37.9 | 38.0 | 38.1 |
| 25 | F 11c | 38.4 | 38.2 | 38.0 | 38.2 | 38.2 | 38.5 | 38.3 | 38.1 | 38.0 | 37.9 | 38.4 | 38.3 |
| 25 | M 14b | 37.9 | 37.6 | 37.7 | 37.4 | 37.7 | 37.8 | 37.7 | 37.6 | 37.4 | 37.8 | 37.9 | 38.0 |
| | | | Mean esophageal temperature without food and water | | | | | | | | | 1 | |
| -30 | M 15b | 31.7 | 14.5 | | | | | | | | | | |
| -30 | F 12c | 36.3 | 16.8 | | | | | | | | | | |
| -20 | F 8c | 38.8 | 37.9 | 23.9 | | | | | | | | | |
| -20 | F 10c | 37.6 | 37.1 | 20.1 | | | | | | | | | |
| -12 | M 11b | 37.8 | 37.6 | 37.3 | 37.7 | 37.9 | 38.1 | 37.8 | 37.5 | 30.1 | 11.7 | | |
| -12 | F 9c | 38.1 | 38.0 | 38.5 | 38.1 | 37.9 | 38.3 | 38.3 | 32.2 | 14.6 | | 25.4 | |
| 0 | M 12b | 37.8 | 37.9 | 37.6 | 37.3 | 37.1 | 37.0 | 38.0 | 37.7 | 37.5 | 37.5 | 37.4 | 37.4 |
| 0 | M 13b | 38.4 | 38.6 38.1 | 38.7 | 38.8 38.0 | 38.6 38.0 | 38.2 38.5 | 38.1 | 38.0 | 38.4 37.8 | 38.1 38.1 | 38.5 38.1 | 38.4 |
| 26 25 | F 11c M 14b | 37.9 | 37.5 | 38.2 | 38.1 | 38.0 | 37.9 | 37.9 | 37.7 | 37.9 | 37.6 | 37.5 | 37.6 |
| 23 | JV1 140 | 57.0 | 57.5 | 30.4 | 50.1 | 00.0 | 51.5 | 51.5 | 01.1 | 01.9 | 01.0 | 01.0 | 07.0 |

ment. The mean body core temperature seems to lie between 37° and 38° C. The body temperature of all female mice averaged 0.5° C. higher than that of males, although in a few cases individual means were lower. The complete range of variability of body temperature in the mice measured was from 2.1° to 4.5° C. with a mean of 3.0° in the females, and from 0.8° to 3.8° C. with a mean of 2.6° in the males. Variation in body temperature became very much reduced when the mice were quiet and body temperature fluctuations were then in the neighborhood of $\pm 0.5^{\circ}$ C.

Esophageal and subcutaneous temperature differences. It is well known that gradients in temperature exist between the interior of the body and the surface or subcutaneous area, due to differences in rates of heat loss and heat production in these regions. The difference between subcutaneous and esophageal temperatures in white-footed mice was determined by alternately measuring esophageal and subcutaneous temperatures at approximately half-minute intervals with an indicator potentiometer. While at room temperature, temperatures were recorded from the

| with and without food and water | | | | | | | | | | | | |
|---------------------------------|--|--|---|---|---|--|---|--|---|---|---|---|
| | | Hour of Exposure | | | | | | | | | | |
| Sex and number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | | Mean subcutaneous temperature with food and water provided | | | | | | | | | | |
| F 1c | 36.3 | 26.4 | 10.7 | | | | | | | | | |
| | | | | | | | | | | | | } |
| | | _ | | 35.9 | 36.9 | 37.0 | 37.3 | 37.0 | 36.5 | 36.7 | 36.8 | 37.1 |
| | 1 | | | 38.7 | 38.3 | 37.9 | 37.4 | 37.4 | 37.6 | 36.9 | | 35.8 |
| M 4b | 39.1 | 38.1 | 37.5 | 37.4 | 36.8 | 36.6 | 34.1 | 34.1 | 33.9 | 29.5 | 4.6 | |
| F 3c | 35.8 | 37.1 | 38.6 | 38.6 | 38.3 | 37.9 | 38.2 | 37.8 | 36.6 | 35.4 | 26.3 | 4.1 |
| | | | | | | | | (| | | | 38.2 |
| | | | | | | | | | | 1 | | 37.8 |
| | 1 | | | | • | , | | 1 | | 1 | | 37.2 |
| F 4C | 31.9 | 38.0 | 38.0 | 30.1 | 30.3 | 30.1 | 31.9 | 31.0 | 51.1 | 31.0 | 37.0 | 31.9 |
| | | Mean subcutaneous temperature without food and water | | | | | | | | | | |
| | | | | | | | | | | | | |
| | | | | | | | | | | | | |
| | | | 10 5 | | | | | | | | | |
| | | , | 1 | | | | | | | | | |
| | | | | | | | | | | | | |
| | | | | 33.5 | 36.6 | 34.3 | 11.9 | | | | | |
| M 9b | 37.2 | 36.4 | 36.7 | 35.7 | 35.7 | 38.3 | 37.9 | 30.9 | 12.7 | | | |
| M 6b | 37.2 | 37.7 | 37.4 | 37.3 | 37.0 | 37.8 | 37.5 | 37.4 | 37.7 | 37.6 | 37.3 | 37.6 |
| F 6c | 38.4 | 38.0 | 38.1 | 38.3 | 38.2 | 38.0 | 38.5 | 38.3 | 38.4 | 38.1 | 38.1 | 38.2 |
| М — | 37.6 | 37.7 | 36.1 | 37.0 | 36.8 | 36.9 | 36.3 | 37.0 | 36.5 | 36.2 | 37.3 | 39.3 |
| F — | 37.0 | 36.9 | 37.3 | 37.2 | 37.7 | 37.7 | 38.3 | 38.6 | 38.1 | 37.9 | 38.0 | 38.0 |
| | number F 1c M 1b M 2b M 3b F 2c M 4b F 3c F 3c F 4c M 1b F 4c F 5c M 5b F 6c M 6b M 9b M 6b F 6c | number 1 F 1c 36.3 M 1b 37.2 M 2b 32.4 M 3b 36.5 F 2c 37.5 M 4b 39.1 F 3c 35.8 F 3c 38.4 F 4c 37.7 M 1b 37.4 F 4c 37.9 F 4c 37.9 F 5c 30.8 M 5b 29.7 F 6c 38.2 M 6b 37.3 M 8b 33.9 M 9b 37.2 M 6b 37.6 | number 1 2 F 1c 36.3 26.4 M 1b 37.2 25.7 M $2b$ 32.4 28.5 M $3b$ 36.5 36.7 F $2c$ 37.5 38.7 M $4b$ 39.1 38.1 F $3c$ 35.8 37.1 F $3c$ 35.8 37.1 F $3c$ 38.4 38.2 F $4c$ 37.7 37.8 M $1b$ 37.4 37.2 F $4c$ 37.9 38.0 $$ | $ \begin{array}{c c c c c c c c c c c c c c c c c c c $ | $ \begin{array}{ c c c c c c c c c c c c c c c c c c c$ | $\begin{tabular}{ c c c c c c c c c c c c c c c c c c c$ | $ \begin{array}{ c c c c c c c c c c c c c c c c c c c$ | Hour of Exposur Sex and number 1 2 3 4 5 6 7 Mean subcutaneous temperature with f F 1c 36.3 26.4 10.7 9.9 7 M 1b 37.2 25.7 9.9 7 7 7 M 2b 32.4 28.5 5.3 7 36.9 37.0 37.3 F 2c 37.5 38.7 39.1 38.7 38.3 37.9 37.4 M 4b 39.1 38.1 37.5 37.4 36.8 36.6 34.1 F 3c 35.8 37.1 38.6 38.6 38.3 37.9 38.2 F 4c 37.7 37.8 37.6 37.8 37.9 38.0 M 1b 37.4 37.2 37.1 37.6 37.5 37.4 F 4c 37.7 37.8 37.6 37.8 37.9 38.0 M 1b 37.4 37.2 37 | Hour of Exposure Sex and number 1 2 3 4 5 6 7 8 Mean subcutaneous temperature with food and F 1c 36.3 26.4 10.7 8 8 M 37.2 25.7 9.9 8 8 8 8 8 9 37.0 37.3 37.0 M 3b 36.5 36.7 36.0 35.9 36.9 37.0 37.3 37.0 F 2c 37.5 38.7 39.1 38.7 38.3 37.9 37.4 37.4 M 4b 39.1 38.1 37.5 37.4 36.8 36.6 34.1 34.1 F 3c 35.8 37.1 38.6 38.6 38.3 37.9 38.2 37.8 F 3c 37.7 37.8 37.6 37.5 37.4 37.2 F 4c 37.7 38.0 38.0 38.1 | Hour of Exposure Sex and number 1 2 3 4 5 6 7 8 9 Mean subcutaneous temperature with food and water provided and water provided and the provid | $ \begin{array}{ c c c c c c c c c c c c c c c c c c c$ | Hour of Exposure Sex and number 1 2 3 4 5 6 7 8 9 10 11 Mean subcutaneous temperature with food and water provided F 1c 36.3 26.4 10.7 9.9 3.4 3.5 6 7 8 9 10 11 Mean subcutaneous temperature with food and water provided Mean Subcutaneous temperature with food and water F for Stress and for the stress and |

TABLE IV

Subcutaneous temperatures of Peromyscus leucopus noveboracensis in relation to air temperature with and without food and water

same animals when under light anaesthesia and two hours after recovery from anaesthesia (Table II). Individual differences between esophageal and subcutaneous temperatures ranged from 0.4° to 1.7° for anaesthetized animals and from 0.9° to 1.7° for those which had recovered from anaesthesia. The mean difference between subcutaneous and esophageal of anaesthetized animals was the same as that of animals which had recovered from anaesthesia.

No simultaneous comparisons between esophageal and subcutaneous body tem-

peratures were made at low air temperatures, but some idea of the relationship between the two temperatures in active, unanaesthetized animals can be obtained by comparing individual determinations of esophageal and subcutaneous temperatures at different air temperatures (Tables III and IV). However, as the same individuals were not used in the two series of determinations, temperature differences cannot be determined for individual mice.

Body temperature in relation to cold stress. Both esophageal and subcutaneous temperatures were determined at different degrees of low temperature and both

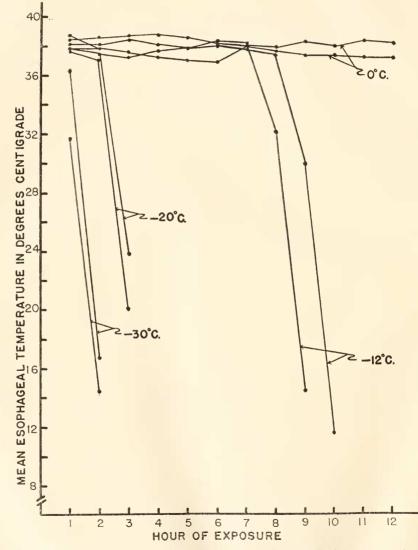


FIGURE 1. Mean esophageal temperatures of eight adult *Pcromyscus leucopus noveboracensis* subjected to cold stress (0° C. to -30° C.) when deprived of food and water.

with and without food and water. Continuous measurements of subcutaneous temperature were made, while esophageal temperatures were recorded within a 10minute period outside the low temperature chamber after which the animals were again placed at low temperature. The possibility exists that this disturbance may have significantly altered the esophageal temperature readings. The esophageal temperature for each individual was determined at room temperature before subjecting it to lower temperatures. The mean temperature after the first hour of exposure was then averaged with the mean esophageal temperature at room temperature to give the mean temperature during the hour. The mean temperature at the end of each successive hour of exposure was then averaged with that at the end of the preceding hour in a similar fashion. Average subcutaneous temperatures were computed from automatically recorded subcutaneous temperatures for each hour of exposure. Plus and minus variations, which were of the order $\pm 0.5^{\circ}$ C, tend to cancel each other out so that these averages are considered to be quite accurate.

Animals which were used more than once were kept at room temperatures for one to three days before exposing them to low temperatures again. None of the animals were exposed to low temperatures for more than 12 hours at a time, and those animals which were exposed to temperatures below 0° C. were held at room temperature for at least two days before they were again subjected to low temperature.

With but two exceptions, all individuals which were provided with food and water maintained quite uniform subcutaneous and esophageal temperatures during the entire 12-hour period of exposure at room temperatures down to about -25° C. At temperatures around -30° C, the mice in nearly all cases became hypothermic before the end of the first hour of exposure. When food and water were withheld the mice maintained constant temperatures during the 12-hour period only at air temperatures above 0° C. (Tables III and IV). Figure 1 shows the relationship between esophageal temperature, air temperature, and length of exposure at various degrees of low temperature with food and water withheld. Essentially the same relationship holds for subcutaneous temperatures of animals exposed to low temperature in the absence of food and water.

Some mice showed a very gradual rise in the mean body temperature during initial exposure to cold. This rise in body temperature was probably associated with an elevation of metabolism caused by exposure to low temperature as reported by a number of investigators (Adolph, 1950; Adolph and Lawrow, 1951; Benedict and MacLeod, 1929; Bodansky and Duff, 1936; Gosselin, 1949; Hart, 1950; Horvath *et al.*, 1938; Penrod, 1949; and others).

DISCUSSION

When subjected to sufficiently low air temperature all mammals will eventually undergo a lowering of body temperature from which recovery is possible if the body temperature stays within the animal's tolerable range of hypothermia. The limits of this range vary with the duration and severity of the low temperature to which the mammal is exposed. Determinations of normal body temperatures and lower lethal temperatures for several species of mammals (Haterius and Maison, 1948; Luyet and Gehenio, 1940; Scott and Bazett, 1941; Wislocki, 1933) show that the tolerable range of hypothermia is often wide, ranging from about 13° to 37° C. For most species of mammals, including the white-footed mouse, *Peromyscus leucopus*, the tolerable range is somewhere between 20° and 25° C.

The lower lethal limits of body temperature in different species of rodents vary considerably. Hart (1951a) recorded lethal colonic temperatures from 11 deer mice, *Peromyscus maniculatus*, which ranged from 0.6° to 13.9° C. with an average of 9.2° C. The mean lethal temperature of 4.6° C. for *Peromyscus leucopus* determined in this study is considerably lower although the criteria of lethality may have varied. A Palestinian mouse, *Meriones tamaricinus*, was found to have a lower lethal temperature of about 13° C. (Bodenheimer, 1949). Lethal body temperatures of 8 white mice averaged 10° C. (Hart, 1951a). Lower lethal limits for the white rat (Adolph, 1948) and the guinea pig (Gosselin, 1949) are somewhat higher than for mice, while that of the hamster (Adolph and Lawrow, 1951) is considerably lower.

Species differences and differences in methods of measuring the lethal point undoubtedly account for much of the variation in lower lethal body temperatures of similar sized rodents. Other factors which may alter the lethal temperature are sex, amount of activity, nutritive state, relative humidity and previous acclimation to high or low temperatures. Thus the range of tolerance may vary to some extent depending upon the conditions of the experiment.

The range of tolerance above average body temperatures for most of the smaller species of rodents appears to be about the same. Data on normal body temperatures and upper lethal temperatures for the rabbit and dog (Heilbrunn, 1943; Wislocki, 1933) give tolerable ranges of hyperthermia from 4.0° to 7.5° C. The range is somewhat wider for the echidna and sloth (Britton and Atkinson, 1938; Enders and Davis, 1936; Martin, 1902, 1930; Morrison, 1945; Sutherland, 1897) in which it is between 5° and 9° C.

It seems evident from the present study that an adequate supply of food and water is important in avoidance of hypothermia at low temperatures. In addition, behavior responses such as huddling, burrowing and nest-building enable small mammals to avoid hypothermia at very low ambient temperatures (Kinder, 1927; Richter, 1927, 1942; Scholander, Walters, Hock and Irving, 1950; Sealander, 1952).

Behavior adjustments are possibly of even greater importance in avoidance of hyperthermia at high ambient temperatures. These include postural adjustments to expose greater body surface, spreading of saliva on the fur (Herrington, 1940, and this study) and decreases in amount of motor activity. According to Sumner (1925) small desert mammals have no special ability to resist high temperatures but are nocturnal in activity and remain in their burrow system during the hotter part of the day. Adjustments of this sort are more easily made than changes in the animal's energy balance.

SUMMARY

1. Observations were made on behavior responses and body temperatures of white-footed mice, *Peromyscus leucopus noveboracensis*, subjected to ambient temperatures ranging from -35° C. to $+50^{\circ}$ C.

2. Behavior responses to low temperature included gnawing, grooming movements, running, rapid breathing and shivering. Motor activity was greatest upon initial exposure to cold and at moderately low temperatures (0° to -20° C.) and decreased almost entirely at lower temperatures $(-20^{\circ} \text{ to } -35^{\circ} \text{ C})$. Behavior responses to high temperatures involved a decrease in activity and assumption of postures which exposed the maximum body surface area. Salivation occurred quite freely at temperatures between 40° and 50° C.

3. The lowest minimal recoverable body temperature observed was 10° C. This was an esophageal temperature when the mouse was exposed to air temperatures ranging from -23° C. to -12° C. over a period of 65 minutes. Activity was minimal during the entire period of exposure.

4. The mean lower lethal body temperature (esophageal) was $4.6^{\circ} + 0.5^{\circ}$ C. (15 determinations). Lower lethal body temperatures ranged from 3.5° to 5.0° C. The lower lethal body temperatures were determined at ambient temperatures ranging from -12° to -35° C, and the duration of exposure before death occurred varied from 45 minutes to 8.5 hours. There was, however, no apparent correlation between the lower lethal body temperature and the duration of exposure or ambient temperature. Upper lethal body temperatures of two mice were between 43° and 44° C.

5. At room temperatures esophageal temperatures ranged from 35.5° to 40.5° C. with a mean of 38.1° C, for males, and from 35.4° to 40.5° C, with a mean of 37.6° C. for females. The difference between sexes may not be significant.

6. Differences between esophageal and subcutaneous body temperatures of individual mice ranged from 0.4° to 1.7° C. The mean difference of 1.2° C. for seven mice remained the same under light anaesthesia although both esophageal and subcutaneous temperatures were subnormal.

7. Body temperatures of mice supplied with food and water remained rather constant when the mice were subjected to cold stress, except at ambient temperatures around -30° C. When food and water were withheld all mice became hypothermic within 12 hours at all temperatures below -1° C. These findings indicate that ordinary low temperatures may not be critical for small mammals in nature unless they are combined with lack of food, water and possibly shelter. Behavior responses such as huddling, burrowing and nest-building may give enough additional protection to offset most of the adverse effects of low air temperatures.

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